

Decline in species richness and cover of exotic plants with increasing altitude

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Abstract

Increasing altitude can result in reduced diversity of exotic plants while disturbance usually benefits exotics. Species richness and cover of exotics was examined in paired 120 m² roadside and adjacent natural vegetation plots at 10 sites along a 1000 m altitudinal gradient from montane to the alpine zone in the Snowy Mountains. Species richness and cover of exotics decreased linearly with increasing altitude in both habitats. The effect of altitude was partly off set by disturbance, with more species and greater cover of exotics on roadside plots. There was high diversity of annual/biennial forbs particularly at low altitude, and few exotic annuals/biennials above 1510 m. The decline in diversity with altitude may be due to differences in disturbance history, with the highest plots having lower levels of use, but the decline in diversity is most likely due to differences in environmental conditions with increasing altitude that limit exotics, particularly annuals/biennials. (*The Victorian Naturalist* 125 (3), 2008, 64-75)

Introduction

Currently there is debate about the causes of patterns in species richness including which factors account for a commonly observed decrease in species richness with increasing altitude (Rahbek 1995; Körner 2002). For example, a pattern of decreasing diversity of exotic plant species with increasing altitude has been found in several mountain regions including south-central Chile (Pauchard and Alaback 2004), the Swiss Alps (Becker *et al.* 2005) and the northwest mountains in North America (Parks *et al.* 2005). Some studies suggested that climate was a major factor affecting the diversity of exotic plants, while others also considered factors such as a lag effect associated with the dispersal of exotics from valleys or differences in the patterns of human disturbance at higher altitudes as important (Pauchard and Alaback 2004).

In addition to the effects of altitude on species richness, many studies have found that human disturbance benefits exotics including in mountain regions (Lozon and MacIsaac 1997; Jesson *et al.* 2000; Johnston and Pickering 2001; McDougall 2001; Becker *et al.* 2005; Godfree *et al.* 2004; Parks *et al.* 2005; Hill and Pickering 2006). Disturbance in mountain regions has facilitated the introduction of exotics,

both accidentally (by vehicles, in horse feed etc.) and deliberately (rehabilitation/revegetation) (Mallen-Cooper 1990; Jesson *et al.* 2000; Tsuyuzaki 2002; Pauchard and Alaback 2004; McDougall *et al.* 2005). Disturbance also favours the spread of exotics through alteration of habitats. Disturbed sites such as road verges are often characterised by low cover of native vegetation (potentially reducing competition, and providing safe sites for establishment), as well as increased nutrient availability and moisture (Jesson *et al.* 2000; McDougall 2001; Johnston and Johnston 2004; Johnston 2005; Hill and Pickering 2006). For example, in the Snowy Mountains in the Australian Alps, there is a strong association between exotic plants and human disturbance, with most exotic species occurring along roadsides and around buildings (Costin 1954; Mallen-Cooper 1990; Johnston and Pickering 2001; Bear *et al.* 2006).

Determining what may be limiting exotic diversity is particularly important in mountain regions, as temperatures are likely to increase, and snow cover decrease with climatic change (Grabherr *et al.* 1994; Hennessy *et al.* 2003; Pickering *et al.* 2004). Therefore, if climate is currently a

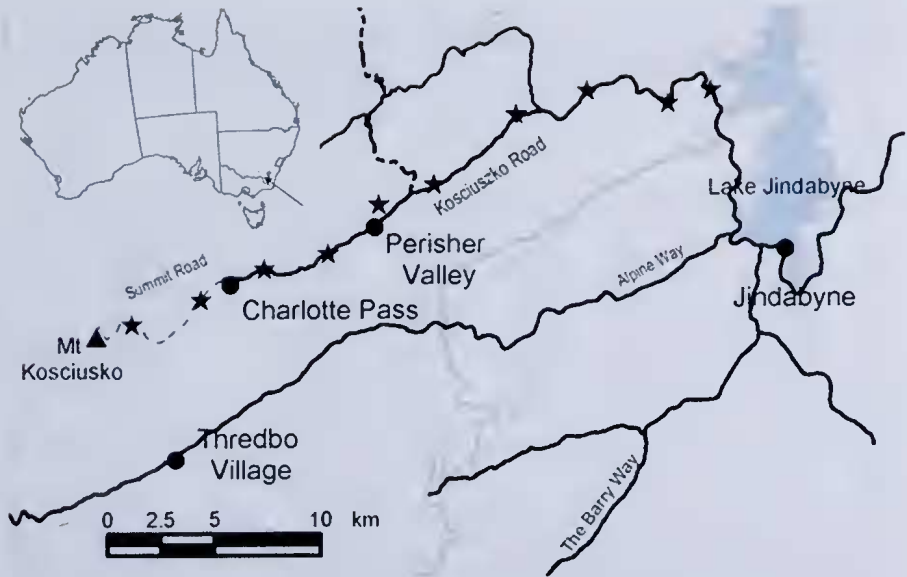


Fig. 1. Location of the 10 sites used to sample exotic species richness and cover in roadside and adjacent paired plots over an altitudinal gradient in the Snowy Mountains, Australia.

limiting factor for exotic species richness in these regions, warming conditions could result in a greater risk of biological invasions (Pickering *et al.* 2004).

This study examines the effect of altitude and disturbance on exotic species richness. Specifically, the diversity and percentage cover of exotic species in paired sites along roadsides and in adjacent native vegetation were compared along an altitudinal gradient in the Snowy Mountains in Australia. It was hypothesised that:

- (1) species richness and cover of exotics would decline with increasing altitude in both roadsides and adjacent plots.
- (2) As disturbance is likely to benefit exotics, including at high altitude, species richness and cover of exotic plants would be greater on roadsides than in adjacent plots; and
- (3) any decline in species richness and cover of exotics with increasing altitude would, at least in part, be offset by disturbance.

Determining the diversity of exotics and what factors are important in limiting their establishment and spread is critical for the management of biological invasions in mountain regions.

Methods

Study area

The Snowy Mountains in Kosciuszko National Park are located in south-eastern Australia and are part of the Australian Alps (Fig. 1). There are three main floristic zones: montane, subalpine and alpine, which are strongly correlated with altitudinal/climatic gradients and which contain distinctive vegetation communities (Costin 1954; Good 1992).

The montane zone occurs between ~500 m and ~1500 m (Good 1992) and is dominated by *Eucalyptus pauciflora* alliance woodlands in association with other *Eucalyptus* species. Construction and maintenance of dams, powerlines, buildings and both sealed and gravel roads are the primary sources of anthropogenic disturbance in the montane zone, associated with a major hydroelectric scheme and tourism (ISC 2004).

The subalpine zone occurs between the lower winter snow line at ~1500 m and the climatic limit of tree growth at ~1850 m. There is continuous snow cover for at least one month per year. The dominant vegetation type is *Eucalyptus niphophila* woodland interspersed with areas of bog, fen, heath and subalpine grasslands. Visitor

Table 1. Details of the 10 sites sampled along the Kosciuszko Road in the central region of the Snowy Mountains, Australia.

Site #	Vegetation zone	Northing	Easting	Altitude (m)	Aspect (°)	Slope (°)	Road type	Distance from road surface to adjacent plot (m)
1	montane	5976000	642000	1020	80	8	sealed	15
2	montane	5975400	640000	1220	Flat	0	sealed	17
3	montane	5976000	636200	1440	290	8	sealed	24
4	subalpine	5974790	132850	1510	275	1	sealed	12
5	subalpine	5971650	629000	1580	290	10	sealed	11
6	subalpine	5970700	626400	1720	20	4	sealed	28
7	subalpine	5968400	624000	1780	170	4	sealed	14
8	subalpine	5967700	621000	1785	165	10	sealed	17
9	alpine	5966250	618000	1880	280	18	gravel	7*
10	alpine	5965100	614750	2020	120	11	gravel	8*

* Distance from edge of plant colonisation on road surface of physical roadside disturbance in alpine plots.

traffic (vehicular, skiing and trampling), ski resort infrastructure and maintenance of roads and ski slopes are major sources of disturbance in this zone (ISC 2004).

The alpine zone occurs above the climatic treeline at ~1860 m to the top of continental Australia's highest mountain, Mt Kosciuszko, at 2228 m and covers an area of approximately 250 km² (Costin *et al.* 2000). The largest contiguous alpine area in the park, and indeed Australia, is the 100 km² around Mt Kosciuszko (Costin 1954; Costin *et al.* 2000). There is snow cover for more than four months per year with a few permanent snowbanks in some years. Low growing shrubs, grasses and herbs characterise the alpine zone (Costin *et al.* 2000; McDougall and Walsh 2007). The main sites of human disturbance in the alpine zone are gravel access roads and gravel, paved, raised steel mesh and informal walking tracks (Worboys and Pickering 2002).

Data on exotic species

Mallen-Cooper surveyed cover and species richness of exotic species in roadside vegetation and in paired adjacent natural vegetation plots at 10 sites located every four km along a 1000 m elevation gradient from the montane zone to the alpine zone in the Snowy Mountains in Kosciuszko National Park in November and December 1983 (Table 1).

All sites were along the Kosciuszko Road, with the lower eight sites along a

public access sealed section of road and the two highest sites along a gravel section of the road which was closed to public vehicles in 1976 and subsequently used as a walking track and for maintenance vehicles (Worboys and Pickering 2002, Fig. 1). As the potential for spread of exotic species is greatest on the downslope of the road (pers obs.) all plots were located on the downslope side of the road.

At each site, one plot was established on the roadside and a paired plot established in the adjacent vegetation. Roadside vegetation was surveyed in 120 m² plots measured from the edge of the road surface (20 m parallel to road x 6 m perpendicular to road) for the lower eight sites, and 30 m parallel to the road x 4 m perpendicular to the road for the two higher sites). Paired plots of the same dimensions were located 5 m from the edge of physical roadside disturbance (as indicated by clearing/cutting etc. of vegetation, presence of foreign material such as gravel etc.) in relatively natural vegetation, ranging from 11 m to 28 m from the road surface itself (Table 1). This distance ensured the potential for weed seed to disperse into the adjacent plots, but was far enough away to minimise the level of direct physical disturbance associated with the road.

For each plot the following variables were recorded:

- (1) presence of all exotic species;
- (2) overall exotic species richness;
- (3) cover of each exotic species estimated

Table 2. Frequency (number of plots) and average percentage cover of exotic species in roadside and adjacent plots at 10 sites along an altitudinal gradient in the Snowy Mountains Australia.

Family	Frequency			Average cover (%)			
	Total	Road side	Adj.	Total	Road side	Adj.	
Perennial forbs							
<i>Acetosella vulgaris</i>	Polygonaceae	18	10	8	2.050	3.70	0.40
<i>Hypochaeris radicata</i>	Asteraceae	15	8	7	1.105	1.65	0.56
<i>Taraxacum officinale</i>	Asteraceae	15	9	6	0.585	0.91	0.26
<i>Trifolium repens</i>	Fabaceae	11	8	3	3.300	6.45	0.15
<i>Cerastium</i> spp.	Carophyllaceae	10	7	3	0.275	0.40	0.15
<i>Achillea millefolium</i>	Asteraceae	5	5	0	1.100	2.20	0.00
<i>Plantago lanceolata</i>	Plantaginaceae	5	5	0	0.210	0.42	0.00
<i>Trifolium hybridum</i>	Fabaceae	3	2	1	0.325	0.60	0.05
<i>Chondrilla juncea</i>	Asteraceae	3	3	0	0.075	0.15	0.00
<i>Oenothera glazioviana</i>	Onagraceae	2	2	0	0.030	0.06	0.00
<i>Rumex crispus</i>	Polygonaceae	2	2	0	0.030	0.06	0.00
<i>Trifolium pratense</i>	Fabaceae	2	2	0	0.030	0.06	0.00
<i>Juncus articulatus</i>	Juncaceae	1	1	0	0.025	0.05	0.00
<i>Salvia verbenaca</i>	Lamiaceae	1	1	0	0.025	0.05	0.00
<i>Pieris hieracioides</i>	Asteraceae	1	0	1	0.005	0.00	0.01
Annual and biennial forbs							
<i>Polygonum</i> spp.	Polygonaceae	7	7	0	0.300	0.60	0.00
<i>Myosotis discolor</i>	Boraginaceae	7	4	3	0.280	0.45	0.11
<i>Cirsium vulgare</i>	Asteraceae	7	5	2	0.175	0.25	0.1
<i>Verbascum virgatum</i>	Scrophulariaceae	7	5	2	0.135	0.21	0.06
<i>Trifolium arvense</i>	Fabaceae	5	3	2	2.550	2.10	3.0
<i>Crepis capillaris</i>	Asteraceae	4	2	2	0.350	0.35	0.35
<i>Spergularia rubra</i>	Caryophyllaceae	4	4	0	0.225	0.45	0.00
<i>Peirorhagia nanteuilii</i>	Caryophyllaceae	4	3	1	0.205	0.40	0.01
<i>Lactuca serriola</i>	Asteraceae	4	2	2	0.080	0.06	0.10
<i>Sonchus asper</i>	Asteraceae	4	3	1	0.060	0.07	0.05
<i>Verbascum thapsus</i>	Scrophulariaceae	4	3	1	0.060	0.11	0.01
<i>Tragopogon dubius</i>	Asteraceae	4	3	1	0.020	0.03	0.01
<i>Trifolium campestre</i>	Fabaceae	3	1	2	0.200	0.05	0.35
<i>Erophila verna</i>	Brassicaceae	3	3	0	0.075	0.15	0.00
<i>Trifolium glomeratum</i>	Fabaceae	3	1	2	0.075	0.05	0.10
<i>Centaurium erythraea</i>	Gentianaceae	3	2	1	0.055	0.10	0.01
<i>Comiza albida</i>	Asteraceae	3	2	1	0.055	0.10	0.01
<i>Aphanes arvensis</i>	Rosaceae	3	2	1	0.035	0.06	0.01
<i>Trifolium dubium</i>	Fabaceae	2	2	0	0.175	0.35	0.00
<i>Linaria arvensis</i>	Scrophulariaceae	2	1	1	0.050	0.05	0.05
<i>Medicago lupulina</i>	Fabaceae	2	2	0	0.050	0.10	0.00
<i>Erodium cicutarium</i>	Geraniaceae	2	2	0	0.030	0.06	0.00
<i>Hirschfeldia incana</i>	Brassicaceae	2	2	0	0.030	0.06	0.00
<i>Veronica arvensis</i>	Scrophulariaceae	2	1	1	0.030	0.01	0.05
<i>Anagallis arvensis</i>	Primulaceae	1	1	0	0.025	0.05	0.00
<i>Echium vulgare</i>	Boraginaceae	1	1	0	0.025	0.05	0.00
<i>Sagina apetala</i>	Caryophyllaceae	1	1	0	0.025	0.05	0.00
<i>Viola arvensis</i>	Violaceae	1	1	0	0.025	0.05	0.00
<i>Carduus tenuiflorus</i>	Asteraceae	1	0	1	0.005	0.00	0.01
<i>Chenopodium album</i>	Chenopodiaceae	1	1	0	0.005	0.01	0.00
<i>Melilotus alba</i>	Fabaceae	1	1	0	0.005	0.01	0.00
Perennial grasses							
<i>Dactylis glomerata</i>	Poaceae	10	7	3	6.050	11.70	0.40
<i>Agrostis capillaris</i>	Poaceae	10	10	0	3.905	7.81	0.00
<i>Poa pratensis</i>	Poaceae	8	6	2	1.755	3.45	0.06
<i>Festuca rubra</i>	Poaceae	7	7	0	0.900	1.80	0.00
<i>Anthoxanthum odoratum</i>	Poaceae	7	4	3	0.175	0.20	0.15
<i>Holcus lanatus</i>	Poaceae	4	3	1	0.100	0.15	0.05
<i>Phleum pratense</i>	Poaceae	4	4	0	0.100	0.20	0.00

Table 2. (Contd.)

	Family	Frequency			Average cover (%)		
		Total	Road side	Adj.	Total	Road side	Adj.
<i>Lolium perenne</i>	Poaceae	4	3	1	0.080	0.15	0.01
<i>Paspalum dilatatum</i>	Poaceae	1	1	0	0.025	0.05	0.00
<i>Annual grasses</i>							
<i>Bromus hordeaceus</i>	Poaceae	6	5	1	0.215	0.42	0.01
<i>Aira caryophylllea</i>	Poaceae	5	3	2	1.225	0.90	1.55
<i>Vulpia myuros</i>	Poaceae	5	3	2	1.100	1.85	0.35
<i>Poa annua</i>	Poaceae	5	5	0	0.125	0.25	0.00
<i>Bromus tectorum</i>	Poaceae	3	3	0	0.075	0.15	0.00
<i>Bromus sterilis</i>	Poaceae	2	1	1	0.050	0.05	0.05
<i>Hordeum leporinum</i>	Poaceae	1	1	0	0.025	0.05	0.00
<i>Panicum laevifolium</i>	Poaceae	1	1	0	0.025	0.05	0.00
<i>Poa bulbosa</i>	Poaceae	1	1	0	0.025	0.05	0.00
<i>Vulpia bromoides</i>	Poaceae	1	1	0	0.025	0.05	0.00
<i>Trees and shrubs</i>							
<i>Malus x domestica</i>	Rosaceae	4	2	2	0.020	0.02	0.02
<i>Rosa rubiginosa</i>	Rosaceae	1	0	1	0.025	0.00	0.05

Names as in PlantNet (2006) or Harden (1990-2003). Adj. = adjacent paired plot ~ 5 m from roadside plots.

- using the Braun-Blanquet cover-abundance scale. Cover estimates were converted into the approximate mid point value of each scale for statistical analysis e.g. Braun-Blanquet values of r + 1, 2, 3, 4 and 5 were given percentage cover values of 0.1, 0.5, 3.0, 15.0, 37.5, 62.5 and 87.5 respectively (Barbour *et al.* 1987, Liddle 1997); and
- (4) total percentage overlapping cover of exotics (e.g. sum of cover of each exotic species). From the data for each plot,
- (5) the frequency of each exotic species (measured as the number of plots in which the species was recorded) and
- (6) the altitude of the highest of the 10 sites in which the species was found (maximum altitude) was calculated.

Statistical analysis

To determine if species richness and cover of exotics varied with disturbance and altitude, a series of one-way ANCOVA were conducted (in SPSS 12.0) with 'treatment' (roadside vs adjacent plots) as the independent variable, and altitude as the covariate. Dependent variables were:

- (1) exotic species richness;
- (2) percentage overlapping cover of exotics;
- (3) species richness of exotic perennial forbs;

- (4) overlapping cover of exotic perennial forbs;
- (5) species richness of exotic annual/biennial forbs;
- (6) total overlapping cover of exotic annual/biennial forbs;
- (7) species richness of exotic perennial grasses;
- (8) total overlapping cover of exotic perennial grasses;
- (9) species richness of exotic annual/biennial grasses; and
- (10) total overlapping cover of exotic annual/biennial grasses.

ANCOVA in SPSS 12.0 were initially run with an interaction term between altitude and disturbance term included. If there was no significant interaction the ANCOVA was repeated without an interaction term. The form of the relationship between altitude and the dependent variables was tested separately for roadside and adjacent plots using linear regressions.

To determine if there were differences in mean frequency, cover and maximum altitude between those exotic species recorded in the earliest general vegetation surveys of the Snowy Mountains and those recorded more recently, one-way ANOVA were conducted in SPSS 12.0. The independent variable was the date of the earliest publication of a species in the region, a surrogate mea-

Table 3. Results from one-way ANCOVA with the interaction comparing the effect of altitude (the covariate) and disturbance (the independent variable) on species richness (in 120 m² plots) and percentage overlapping cover (~mid-point of Braun-Blanquet cover values) of exotics in paired roadside and adjacent plots surveyed in the Snowy Mountains, Australia. Due to the large number of analyses performed on data from the same sites, a more conservative alpha < 0.01 level of significance was used. F and P values for the interaction were only included for significant interactions.

	Interaction		Disturbance		Altitude	
	F	P	F	P	F	P
Species richness						
Total exotic species richness			33.477	<0.001	75.737	<0.001
Perennial exotic forbs			21.282	<0.001	17.616	0.001
Annual/biennial exotic forbs			7.980	0.012	53.980	<0.001
Perennial exotic grasses			25.737	<0.001	5.901	0.027
Annual/biennial exotic grasses	11.344	0.004	17.031	0.001	55.349	<0.001
Percentage cover						
Total for all exotics			38.870	<0.001	27.231	<0.001
Perennial forbs			29.096	<0.001	1.313	0.268
Annual/biennial forbs			1.759	0.202	43.339	<0.001
Perennial grasses			11.942	0.003	1.179	0.293
Annual/biennial grasses			1.609	0.222	20.795	<0.001

survived for the length of time the species has been present in the region. It had four levels: 1898 (7 species), 1954 (20 species), 1981 (26 species) and 1990 (data were collected in 1983, but published in 1999, 12 species). The dependent variables were the frequency (total number of plots in which a species was found), percentage overlapping cover and maximum altitude. Differences between means were examined using Tukey's post-hoc tests.

Assumptions of homogeneity of variance and normal distributions were tested prior to analysis. Frequency (converted to a proportion) and percentage cover data were arcsine transformed. Due to the large number of analyses performed on data from the same sites, a conservative significance of $\alpha < 0.01$ was used for all tests.

Results

Characteristics of exotic species

A total of 67 exotic species were recorded in the 20 plots surveyed (Table 2). Most were annual/biennial forbs (31 species) with just one species of shrub and one tree (Table 2). The families with the highest species richness were the Poaceae (19 species), Asteraceae (12 species) and Fabaceae (nine species). Many species were recorded infrequently (e.g. each of 17 species were found only once) and at low cover. Only seven species occurred in 10 or more sites: the perennial forbs *Acetosella vulgaris*, *Hypochoeris radicata*,

Taraxacum officinale, *Cerastium* spp. and *Trifolium repens*, and the perennial grasses *Agrostis capillaris* and *Dactylis glomerata* (Table 2).

Effect of altitude

With increasing altitude, the total cover and species richness of exotics decreased on both roadside and adjacent plots (Fig. 2, Tables 3 and 4). The rate of decline was similar between the two plots (no significant interaction, Table 3), although the total number of exotic species was lower on the adjacent plots (Fig. 2, Tables 3 and 5).

How exotic species richness and cover changed with increasing altitude differed depending on the life form/life history of the exotics. For perennials there was either a linear decline or no significant effect of altitude. The only significant linear regressions were for species richness and cover of perennial exotic forbs on adjacent plots (Fig. 3a, Tables 3 and 4). For perennial grasses, and perennial forbs on roadsides, there was no significant effect of altitude (Fig. 4, Table 4).

For annual/biennial exotic forbs and grasses, in contrast, there appeared to be a threshold effect of altitude for both roadside and adjacent plots, with very low cover values and species richness values above 1510 m altitude (Figs 3b and d, 4b and d). Although there were significant linear regressions with altitude (Tables 3 and 4), the distribution of values appear more

Table 4. Linear regressions testing the effect of altitude (in m asl x 10⁻³) on species richness (in 120 m² plots) and percentage cover (~mid-point of Braun-Blanquet cover values) of exotics in paired roadside and adjacent plots surveyed in the Snowy Mountains, Australia.

	Plots	Formula	F	P	r ² -adj.
Species richness					
Total exotic species richness	roadside	d = 89.634 - 43.143 x a	69.390	<0.001	0.884
	adjacent	d = 48.109 - 25.452 x a	33.010	<0.001	0.781
Perennial exotic forbs	roadside		7.622	0.025	
	adjacent	d = 10.112 - 4.520 x a	14.600	0.005	0.602
Annual/biennial exotic forbs	roadside	d = 47.030 - 27.026 x a	49.438	<0.001	0.843
	adjacent	d = 25.377 - 14.213 x a	19.556	0.002	0.673
Perennial exotic grasses	roadside		2.132	0.182	
	adjacent		5.437	0.048	
Annual/biennial exotic grasses	roadside	d = 14.914 - 7.781 x a	37.403	<0.001	0.802
	adjacent	d = 5.277 - 2.931 x a	18.902	0.002	0.662
Percentage cover					
Total exotic cover	roadside	pc = 2.070 - 0.818 x a	10.166	0.013	0.505
	adjacent	pc = 1.279 - 0.641 x a	26.873	0.001	0.742
Perennial exotic forbs	roadside		0.188	0.679	
	adjacent	pc = 0.343 - 0.117 x a	26.624	0.001	0.740
Annual/biennial exotic forbs	roadside	pc = 0.994 - 0.476 x a	27.639	0.001	0.747
	adjacent	pc = 0.889 - 0.444 x a	15.784	0.004	0.622
Perennial exotic grasses	roadside		0.683	0.432	
	adjacent		5.940	0.038	
Annual/biennial exotic grasses	roadside	pc = 0.951 - 0.465 x a	17.787	0.002	0.628
	adjacent	pc = 0.861 - 0.434 x a	69.390	<0.001	0.884

adj. = adjusted, d = species richness, pc = overlapping percentage cover, a = altitude (in m asl x 10⁻³)

Table 5. Mean species richness ± Standard Error (in 120 m² plots) and overlapping percentage cover (~mid-point of Braun-Blanquet cover values) of exotic species in paired roadside and adjacent plots surveyed in the Snowy Mountains, Australia

	Species richness			Average overlapping cover (%)	
	Total	Roadside	Adjacent	Roadside	Adjacent
Total for all exotics	68	20.8 ± 4.4	7.5 ± 2.8	52.6 ± 11.3	8.7 ± 5.1
Perennial forbs	15	6.5 ± 0.9	2.9 ± 0.5	16.8 ± 3.6	1.6 ± 0.4
Annual/biennial forbs	31	7.1 ± 2.6	2.7 ± 1.6	6.4 ± 3.1	4.4 ± 2.9
Perennial grasses	9	4.5 ± 0.7	1.0 ± 0.4	25.5 ± 8.4	0.7 ± 0.4
Annual/biennial grasses	11	2.5 ± 0.8	0.6 ± 0.3	3.9 ± 2.3	2.0 ± 1.8
Shrubs	1	0	0.1 ± 0.3	0	0.05 ± 0.16
Trees	1	0.2 ± 0.4	0.2 ± 0.4	0.02 ± 0.04	0.02 ± 0.04

consistent with a threshold effect (Figs. 3 and 4). For example, out of the 31 annual/biennial forbs, only six species (*Cirsium vulgare*, *Medicago lupulina*, *Polygonum spp.*, *Spergularia rubra*, *Tragopogon dubium*, and *Verbascum virgatum*) occurred in any roadside plot above 1510 m and only one species on the adjacent plots (*Verbascum virgatum*). Similarly, of the 11 species of annual/biennial grasses, only three species (*Bromus hordeaceus*, *Bromus sterilis*, and *Poa annua*) were found on roadside plots above 1510 m, and only one species (*Bromus sterilis*) in the adjacent plots. In the alpine plots the only annual exotics recorded

were *Spergularia rubra* and *Poa annua* each in one roadside plot with cover of only 0.5%.

Effect of human disturbance

Roadside plots had higher frequency, percentage overlapping cover and total species richness of exotics than plots in the adjacent native vegetation (Tables 2 and 5). Thirty-two species were only recorded on roadside plots while, just three species were limited to plots in adjacent natural vegetation where they were found only in one plot, each at low cover (0.5%).

There were significantly more species of exotic perennial forbs and grasses and exotic annual/biennial grasses in roadside

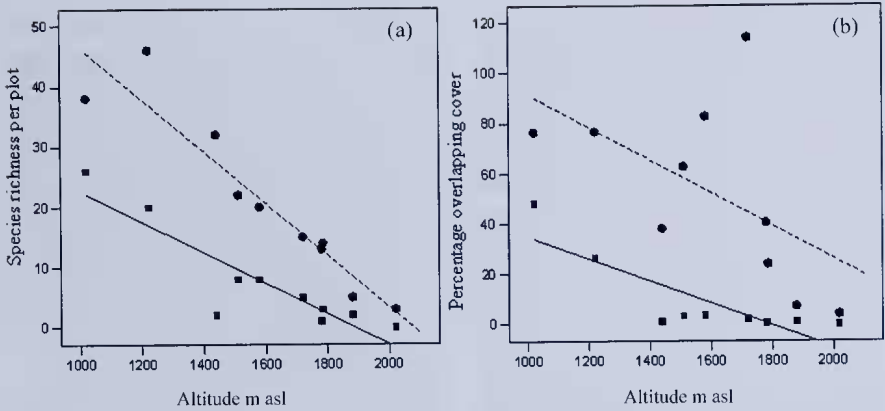


Fig. 2. Total (a) exotic species richness (in 120m² plots) and (b) overlapping percentage cover for all exotic species on paired roadside (circles) and adjacent natural vegetation (squares) plots at 10 sites along an altitudinal gradient in the Snowy Mountains, Australia. The lines are for significant linear regressions for roadside plots (solid line) and adjacent plots (dotted line).

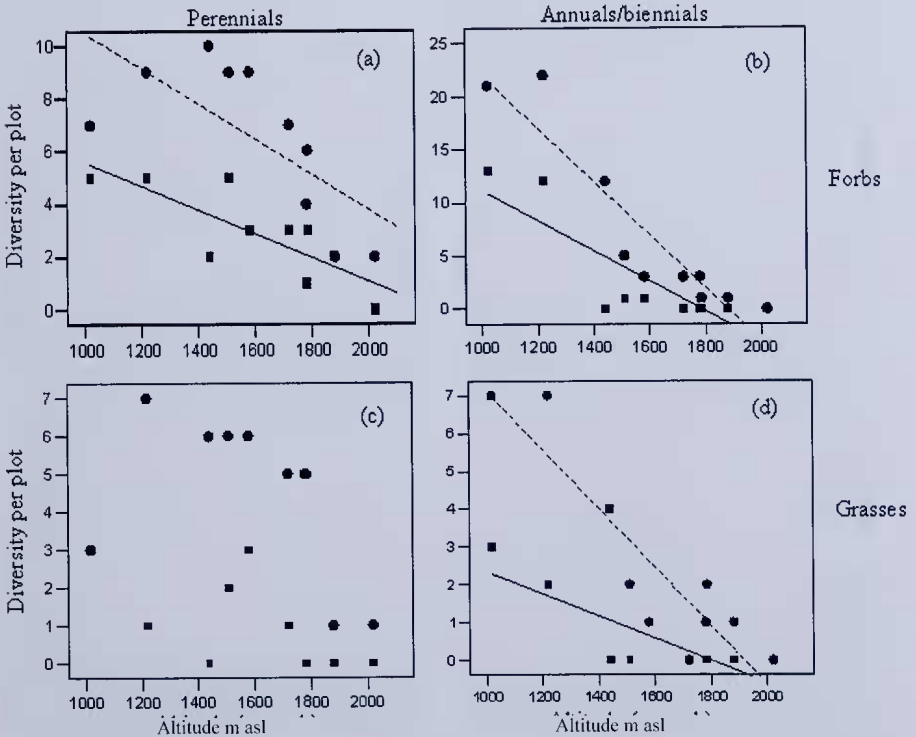


Fig. 3. Total species richness (in 120 m² plots) of (a) exotic perennial forbs (b) exotic annual/biennial forbs (c) exotic perennial grasses and (d) exotic annual/biennial grasses on paired roadside (circles) and adjacent natural vegetation plots (squares) along an altitudinal gradient in the Snowy Mountains, Australia. The lines are for significant linear regressions for roadside plots (solid line) and adjacent plots (dotted line).

plots than adjacent natural vegetation (Tables 3 and 5). The number of annual/biennial forbs did not significantly differ between habitats although in nearly all sites there was higher species richness on the roadside plot (Fig. 3b). The percentage cover of perennial forbs and grasses was significantly higher on roadside plots (Fig. 4, Tables 3 and 5), but there was no significant effect of disturbance detected for cover of annual/biennial forbs and grasses (Fig. 4). Exotic species richness was significantly higher on roadsides (11 species) compared to adjacent plots (8 species, Fig. 2a, Tables 3 and 5, $P < 0.001$). Total cover of exotics was also significantly higher on roadside plots (53%) compared to natural plots (9%) (Fig. 2b; Tables 3 and 5; $p < 0.001$).

Discussion

In our study there was a decline in exotic species richness and cover with increasing altitude. There appeared to be a threshold around the montane-subalpine boundary (~1450-1500 m in the Snowy Mountains) for annual/biennial forbs and grasses, with few if any of these species present above this altitude even in the more favourable roadside plots. This is consistent with the distribution of native annual/biennial forbs and grasses, with very few native annuals in the alpine zone due to the short growing season (Pickering 1997; Costin *et al.* 2000). In contrast, there was no clear pattern for the species richness and percentage cover of perennial grasses with increasing altitude. To determine if the lack of effect of altitude on perennial grasses was not just due to a power effect

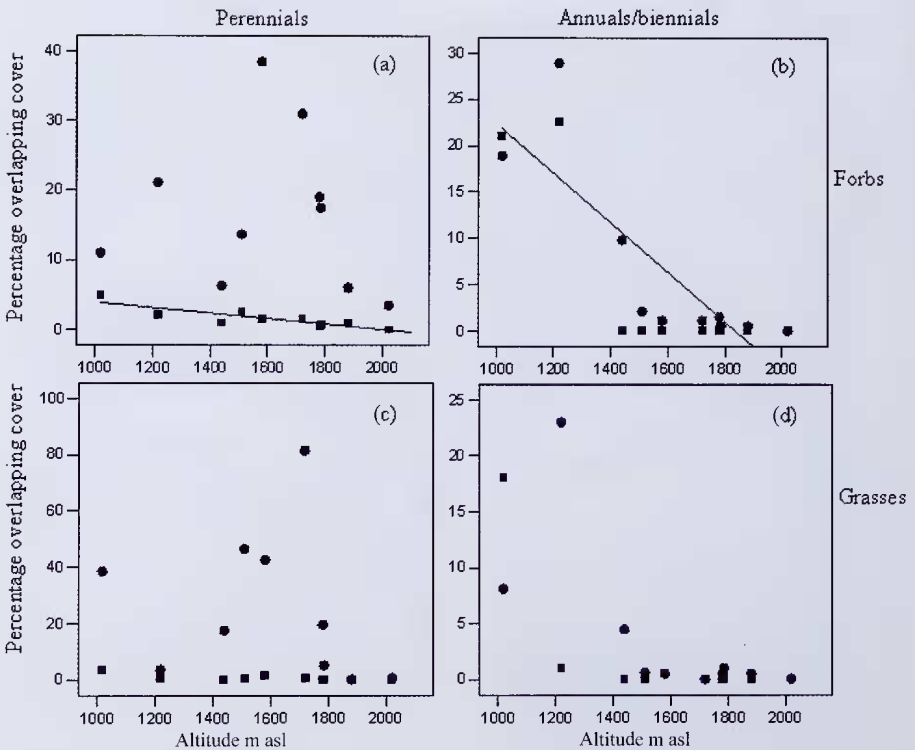


Fig. 4. Total percentage overlapping cover of: (a) exotic perennial forbs (b) exotic annual/biennial forbs (c) exotic perennial grasses (d) exotic annual/biennial grasses on paired roadside (circles) and adjacent natural vegetation (squares) plots along an altitudinal gradient in the Snowy Mountains. The lines are for significant linear regressions for roadside plots (solid line) and adjacent plots (dotted line).

in the analyses, sampling at a larger number of sites along more transects, using a more precise measure of cover is recommended.

There are other observational studies that have examined patterns in species richness of exotics with increasing altitude in mountain regions (Pauchard and Alaback 2004; Becker *et al.* 2005; McDougall *et al.* 2005). These studies also have found declines in total exotic species richness with increasing altitude on roadsides (Pauchard and Alaback 2004; Becker *et al.* 2005) or in natural vegetation in the Australian Alps (McDougall *et al.* 2005). However, unlike our study, they have not compared the patterns between annual/biennials and perennial species to determine if the patterns they found may be due to a lack of exotic annual/biennial species above certain altitudes, as was found here.

There are three possible explanations for a decrease in the species richness and cover of exotics as found here with increasing altitude (Pauchard and Alaback, 2004). First, the decrease in species richness and cover is an ecological effect of the increasing severity of conditions such as climate at high altitude. This is supported by the possible threshold effect of altitude on annual/biennial exotics in this study. It is also supported by a decrease in the species richness of native species in paired native vegetation plots at the same sites (Mallen-Cooper 1990), and in some other mountain regions for native species richness/diversity (Austrheim 2002; Grytnes 2003). This appears to be the most likely explanation for the current pattern.

The second explanation is that extensive human disturbance may have occurred less frequently, less intensively or later at higher altitude sites. This might be the cause of the current pattern with the potential for lower levels of disturbance on roadsides at higher altitude sites. Certainly for the two highest alpine sites, the road is gravel and it has very limited vehicle traffic. Again, additional sampling on this and other roads including ranking different levels of disturbance, and/or manipulative experiments may assist in determining the possible causes of the current patterns in exotic species richness found in this study.

The third explanation is the pattern could be a lag effect, due to exotics dispersing from lowlands to highlands in mountain regions. Decreasing weed diversity and cover along roads within national parks from lowland to highland sites, or along peninsulas, have been found in other studies (Pauchard and Alaback 2004). Further sampling combined with comparing time when first recorded in the region based on herbarium records, would assist in determining if the pattern was due to a lag effect.

Disturbance favours weeds in mountain regions

This study found more exotic species and greater cover of exotics in disturbed plots compared to adjacent plots. The effects of disturbance partly offset the decline in species richness and cover with increasing altitude. For example at the highest site (2020 m altitude), there were no exotics in the natural vegetation, while on the roadside there were *Agrostis capillaris*, *Taraxacum officinale* and *Acetosella vulgaris*.

In this and other studies it is clear that increasing provision of infrastructure for tourism such as roads, tracks and ski resorts favours the establishment and potential spread of exotics (Jesson *et al.* 2000; Johnston and Pickering 2001; McDougall 2001; Johnston and Johnston 2004; Pauchard and Alaback 2004; McDougall *et al.* 2005; Hill and Pickering 2006). However, as seen in this study, natural vegetation, even that adjacent to sites subject to human disturbance, tends to have low cover and diversity of exotics particularly at higher altitude sites (Johnston and Johnston 2004; Hill and Pickering 2006; McDougall *et al.* 2005; Johnston 2005; Bear *et al.* 2006).

The species in this study that were common on roadsides (*Acetosella vulgaris*, *Hypochoeris radicata*, *Taraxacum officinale*, *Cerastium* spp. and *Trifolium repens*, and the perennial grasses *Agrostis capillaris* and *Dactylis glomerata*) are among the most common exotic plants in other surveys of the Snowy Mountains (Mallen-Cooper 1990; Johnston and Pickering 2001; Godfree *et al.* 2004; McDougall *et al.* 2005). They are also part of an international weed flora and can be found in

mountain regions around the world (Jesson *et al.* 2000; Austrheim 2002; Pauchard and Alaback 2004; Parks *et al.* 2005).

Limitations of this study

There are three main limitations to this study:

- (1) it only examined diversity and cover of exotics along one transect at 10 sites along one road in the Snowy Mountains;
- (2) only one site at each altitude was sampled; and
- (3) current patterns of disturbance were not consistent over the transect.

It is likely that vehicle usage decreases with increasing altitude on this road, and the highest two sites were a closed gravel road. However, the general pattern of decreasing species richness with increasing altitude in this study is supported by the results of a more extensive parallel study examining changes in the species richness of native and exotic plants over altitudes on several main roads (16 sites), minor roads (23 sites) and in adjacent native vegetation (25 sites). With a greater number of sites, negative linear relationships were still found for total exotic diversity, supporting the results reported here (Mallen-Cooper 1990, Mallen-Cooper and Pickering, unpublished data). The parallel study, however, did not examine changes in vegetation cover, or examine if there were differences in the patterns depending on the life histories and life forms of the plants.

Climate change and alien plants

Alpine systems are considered to be among the most vulnerable communities to climate change in Australia and overseas (Körner 1999; Hughes 2003; Root *et al.* 2003). There are already data indicating that there has been an increase in species richness, and upward movement in the distribution of native plants in Europe (Grabherr *et al.* 1994). For the Australian Alps, the latest climatic predictions indicate an increase in temperature of between +0.6, and +2.9°C, resulting in between 38-96% decrease in the area receiving at least 60 days of snow cover by 2050 (Henessey *et al.* 2003).

If climate is limiting species richness and abundance of alien plants in the Snowy

Mountains, then predicted declines in snow cover and increasing temperatures will result in more weeds in Australian mountain regions. This is consistent with predictions made in other studies of exotic plants in the Australian Alps (Pickering and Armstrong 2003; Pickering *et al.* 2004; McDougall *et al.* 2005; Bear *et al.* 2006). The potential for an even greater range of weeds with climatic warming emphasises again the need to limit human disturbance in these regions of high conservation value.

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One Hundred and One Years Ago

TIMBER AND TREES

By Ernest Lees, Teacher of Woodwork, Continuation School, Melbourne

The tea-tree (*Leptospermum laevigatum*), on account of its gnarled and twisted trunk, is of little use as timber, but is splendid for fuel, and much sought after by bakers for heating their ovens. It is extremely useful as a break-wind along the coast, and as a sand-binder.

From *The Victorian Naturalist* XXIII, p. 226, March 7, 1907